The contribution of Mediterranean connectivity to morphological variability in Iron Age sheep of the Eastern Mediterranean

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Abstract

The movement of livestock across the Mediterranean is well-documented in the Neolithic era, but its significance during subsequent periods has received less attention. This study explores potential evidence for maritime connections between sheep populations in the Iron Age eastern Mediterranean by analyzing astragal bones from four coastal and inland sites in Israel and Cyprus. Employing an established geometric morphometric protocol, we investigated the hypothesis that intra-site morphological variability is higher in coastal sites, reflecting greater genetic diversity in the livestock populations. While our findings support this hypothesis, the conclusions are constrained by contextual and sample size limitations.

Introduction

The genetic and phenotypic variability of livestock is a multifaceted phenomenon relating, among other things, to a long history of synanthropic mobility (Frantz et al., 2020). Traditionally, most studies on livestock mobility have focused on the spread of domesticated animals across space and through time (Daly et al., 2018; Davis & Simões, 2016; Krause-Kyora et al., 2013; Ottoni et al., 2013). Recent research has also focused on later periods, revealing how local livestock improvement, geographical and cultural isolation, human demographic expansion, and long-distance colonization and trade shaped the rich diversity of livestock populations that rapidly disappeared in the modern period (Fuks & Marom, 2021; Meiri et al., 2017). By tracing subtle dissimilarities between animals from different times and locales, techniques like ancient DNA and geometric morphometrics allow us to perceive some of the genetic and phenotypic patterns in ancient livestock (Colominas Barberà et al., 2019; Evin et al., 2015; Haruda et al., 2019). In this study, we attempt to isolate and identify the contribution of maritime mobility to livestock biological diversity in antiquity by investigating the phenotypic variability of domestic sheep from coastal and inland archaeological sites in the eastern Mediterranean (Muñiz et al., 1995; Valenzuela-Lamas et al., 2018).

This study emerges from the current paradigm underpinning the importance of connectivity in Mediterranean history and archaeology. This paradigm was first put forward explicitly by Horden and Purcell (2000), and its application has been extended to the Bronze and Iron Age Iron Age Mediterranean by the magisterial work of Cyprian Broodbank (2013). It states that constant material exchange between communities was a basic tenant of pre-Modern Mediterranean life. This exchange alleviated the uneven distribution of risk and opportunity between different micro-environments in a chronically unpredictable environment. A deeply-ingrained sociocultural adaptation to the *longue durée* features of Mediterranean geography, exchange was often a maritime affair capitalizing on the advantages of the Sea as a medium for rapid transportation.

But were livestock part of this constant maritime exchange in the Bronze and Iron Ages? Although Mediterranean maritime trade in the Bronze and Iron Ages immediately evokes the riches of the Uluburun shipwreck (Cline & Yasur-Landau, 2007; Pulak, 1998), smaller-scale trade is known from the late second millennium BCE onward in the eastern Mediterranean by

evidence of the mixed cargoes of amphorae, scrap metal and other mundane items found, for example, in the Cape Gelidonya and Point Iria shipwrecks (Bass, 1967; Bass, 1961; Phelps et al., 1999). It is reasonable to presume that livestock were among the goods transported via *cabotage* or larger-scale maritime trade, especially male breeding stock, although concrete osteoarchaeological evidence from a shipwreck is not known before the end of Classical antiquity. Complete bones of a single male sheep were recovered from the Ma‘agan Mikhael B shipwreck, interpreted to be a merchantman wrecked off the Carmel coast in the middle of the 7th century CE. No butchery or consumption marks were found on the bones, which suggest that they represent the remains of an animal transported alive on board (Harding, 2021).

Earlier evidence for maritime trade in livestock in the east Mediterranean exists. For example, a European haplotype observed in the mitochondrial DNA of south Levantine pigs was traced back to an introduction event at the turn of the second millennium BCE (Meiri et al., 2013). Similarly, patterns of greater body size variability were observed in sheep from Iron Age coastal sites in the Levant in two recent biometric studies (Chahoud et al., 2023; Harding et al., 2023). This enhanced variability could be related to the introduction of non-local breeding stock to coastal settlements via maritime trade networks, as suggested in both studies; however, as their authors add, changes in livestock height and robusticity could also result from changes in nutrition, castration, and other herd maintenance, optimization and management practices.

In this study, we directly address the relationship between morphological/phenotypic variation in livestock and access to maritime trading networks in antiquity. To do so, we focused on Iron Age sheep from two coastal and two inland sites in the southern Levant and Cyprus (Figure 1). Our choice of period and region was primed by the aforementioned biometric results suggesting maritime transportation of livestock. We quantified the shape of astragali using a published geometric morphometric protocol that was successfully used to study morphological variability between geographically distinct populations of domestic sheep (or ‘breeds’) (Pöllath et al., 2019). Geometric morphometric analysis is appropriate in this context because it can isolate shape variables from size, allowing us to analyze the phylogenetic signal inherent in shape without confounding it with the patterns observed in size data, which is also affected by ontogenetic history. Although we admit that it is reductive to ascribe shape variability solely to phylogeny and size variability only to human impact on ontogenesis, this simple scheme allows

us to put forth statistically testable hypotheses within the limits of the archaeological materials available to us. As a precaution, we chose samples that derive from sites in a similar topographic setting, to minimize possible functional morphological differences, and we checked for the effect of size differences on shape.

Therefore, we hypothesize that the *variability of shape observed in sheep astragali from coastal sites directly exposed to maritime networks will be higher than those from inland sites.* This hypothesis will be tested by an analysis of morphological disparity on Procrustes transformed landmark data. Morphological disparity is estimated as the Procrustes variance for groups, using residuals of a linear model fit. P-values can be obtained using a random residual permutation procedure. In itself, Procrustes variance is the same sum of the diagonal elements of the group covariance matrix divided by the number of observations in the group (Zelditch et al., 2014, p. 487).

Finally, a note on spatiotemporal resolution is in order. Specialists in the archaeology of the Iron Age Levant are used to fine contextual resolutions and a high, almost decadal-scale temporal record obtained from radiocarbon dating and very refined ceramic chronologies. To them, the approximately five centuries spanned by our sample and the site level contextual resolution may seem too coarse to be meaningful. We can answer such concerns in two ways. The first is by noting the trivial fact that we must pool chronostratigraphic phases in order to even remotely approach a suitable sample size of complete sheep astragali from each site.

The second, which is less trivial, is that we should not assume that the pace of spread of livestock morphotypes is related to the pace of change in ceramic assemblages on which archaeological chronostratigraphy is ultimately based. Cultural evolution is rapid in comparison to biological evolution. We therefore think that the scale of time represented by our samples, which spans a few centuries after the Iron Age explosion of trans-Mediterranean trade, is essentially right for observing the more ‘viscous’ spread of sheep morphotypes across large regions. Nevertheless, we do not purport to have surmounted the issue of insufficient sample sizes and unresolved spatiotemporal scales in our study. Our results, which represent the first study of animal mobility in the southern Levant using geometric morphometric methods, should be somewhat liberally interpreted due to the primacy of this study.

Study sites

Our study sites are spatiotemporally located in the Iron Age and the Persian period (9th-4th centuries BCE) Eastern Mediterranean. This region was a hub of maritime activity during that period, when trans-Mediterranean maritime connections stretched out from the Levantine coast to Gibraltar (Brody, 2002; Broodbank, 2013; Eshel et al., 2018). We expect that this extensive maritime network also includes trade in animals, and therefore these sites provide a suitable setting to explore the link between maritime connectivity and livestock mobility. We focus our efforts on four assemblages chosen because they are in different degrees of remoteness from the sea, and because they have a fair number of astragali from Iron Age contexts, some of which could be identified as sheep.

A) *Tel Abel Beth Maacah (ABM, inland settlement):* Tel Abel Beth Maacah (Tel Abil el Qameh, ABM), is located at the northern Hula Valley (Panitz-Cohen et al., 2013; Yahalom-Mack et al., 2018; Panitz-Cohen and Yahalom-Mack, 2019; Marom et al., 2020). Excavations uncovered a sequence from the Bronze Age through the Ottoman period, with peaks in the MBA and IA1–2a (Panitz-Cohen et al., 2013; Yahalom-Mack et al., 2018). In the IA1–2a (12th–9th centuries BCE), the site was a major urban center (Susnow et al., 2021, with refs.). The GMM sample comes from a hoard of astragali found in an IA2a (10th–9th centuries BCE) cultic context (Susnow et al., 2021).

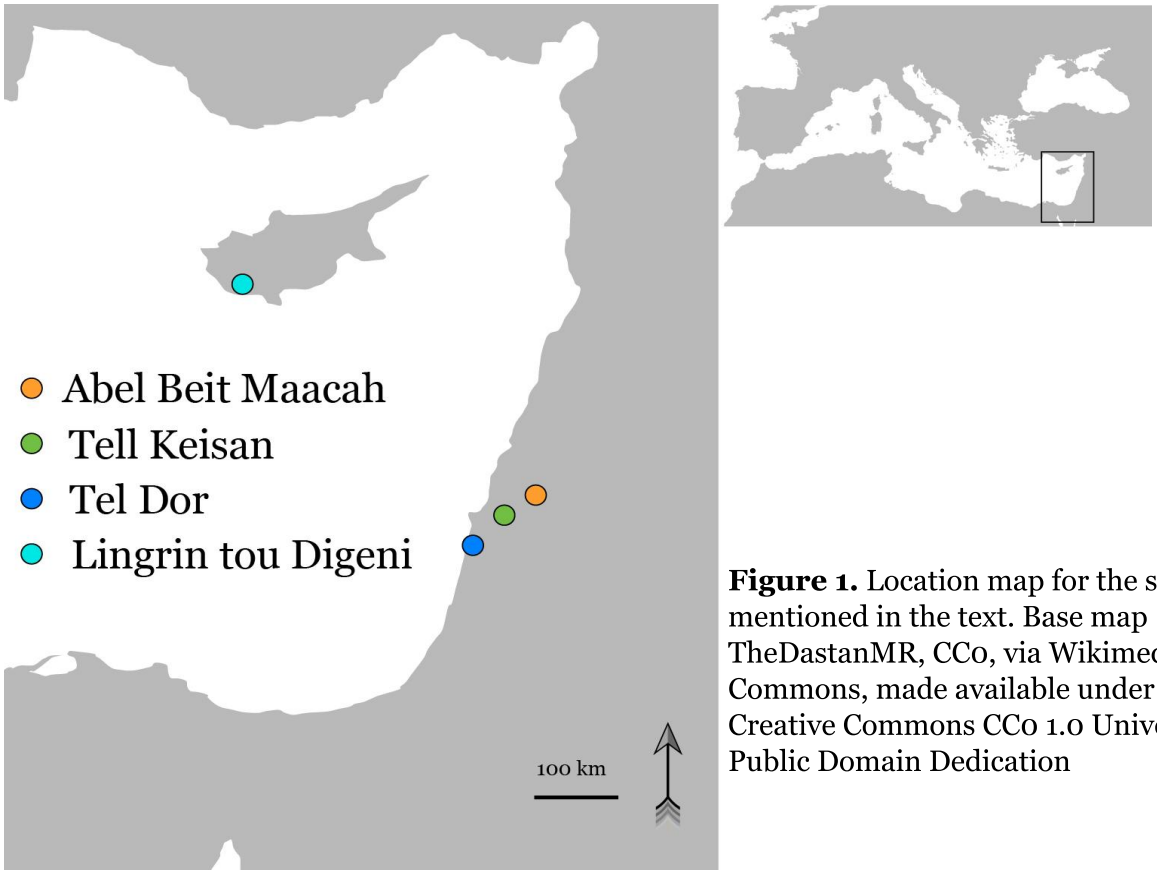

Figure 1. Location map for the sites mentioned in the text. Base map TheDastanMR, CC0, via Wikimedia Commons, made available under the Creative Commons CC0 1.0 Universal Public Domain Dedication

(B) *Tell Keisan (KSN, inland settlement):* Tell Keisan was settled from the Neolithic to the Hellenistic periods, with peaks in the Middle Bronze Age and the Iron Age (Briend and Humbert, 1980; Stern et al., 1993b; Lehmann, 2001; 2021; Lehmann and Peilstocker, 2012). It is located 8 km east of the coastal port city Akko, and served as its agricultural hinterland and a station on the road to the hills of the western Galilee (Stern et al., 1993b; Lehmann and Peilstocker, 2012; Aubet, 2014). Tell Keisan had close ties with Tyre throughout the Iron Age 2 and Persian periods, and a strong 'Phoenician' influence on its material culture (Lehmann and Peilstocker, 2012). The geometric morphometric sample includes materials from deposits dating to the IA2 and the Persian period, which represent general discard of animal bone remains.

(C) *Tel Dor (DOR, coastal settlement):* Tel Dor (Khirbet el-Burj) is located 21 km south of Haifa. It was an important seaside settlement from the Middle Bronze Age through the Byzantine period (Raveh and Kingsley, 1991; Stern et al., 1993a; Nitschke et al., 2011; Gilboa, 2015; Gilboa and Sharon, 2017). Dor has been one of the few natural anchorages along the southern

Levantine coast, and therefore a major port and maritime activity center (Raban, 1981; Wachsmann and Raveh, 1984; Raban and Galili, 1985; Gambash, 2015; Gilboa et al., 2015; Yasur-Landau et al., 2018). The IA sequence at Dor can be divided into two subsequences: the broadly Phoenician 'Early Sequence' (IA1a–IA1|2, c. 1100–850 BCE), with connections to Egypt, Cyprus, and the Mediterranean; and the 'Late Sequence' (IA2a–IA2c, 850–630 BCE) with an inland-facing Israelite administrative center up until the conquest of the Neo-Assyrian empire in 734/2 BCE (Gilboa et al., 2015; Gilboa and Sharon, 2017). The animal economy at Tel Dor remained remarkably stable through time, with a generalized Mediterranean mixed economy dominated by sheep and goat (Raban-Gerstel et al., 2008; Sapir-Hen et al., 2014; Bartosiewicz and Lisk, 2018). The geometric morphometric sample comes from different IA2 contexts in Area D5, which represent general discard of animal bone remains.

(D) *Lingrin tou Digeni (LTD, coastal settlement):* The site of Kouklia-Lingrin tou Digeni (hereafter 'Lingrin tou Digeni') is a sanctuary in Cyprus that dates mainly to the Archaic and Classical periods. Emergency excavations, which took place after looting was reported in the area, revealed extensive evidence of ritual activity in the form of relevant architectural remains (e.g. courtyard with altar), large numbers of votive human and animal figurines, as well as an associated large faunal assemblage (Raptou 2008; 2010). These ritual deposits yielded the sample used for the geometric morphometric analysis.

Materials and methods

The geometric morphometric analysis (GMM; for code and data files see https://zenodo.org/doi/10.5281/zenodo.10276146) was conducted on a sample of sheep astragali that were osteologically mature at time of death, as well as free from surface damage, modifications, burning, pathology, or other anomalies that would inhibit comparison using digital landmarks. Skeletal elements were visually identified as *Ovis* sp. using morphological criteria (Boessneck, 1970; Zeder & Lapham, 2010) and the comparative collection at the Laboratory for Archaeozoology at the University of Haifa.

Site Name	Site Code	Zone	Dating	Sample N=
Abel Beth Maacah	ABM	Inland	Iron Age II (10th–9th c. BCE)	74
Tell Keisan	Keisan	Inland	Iron Age II–Persian Period (950–332 BCE)	14
Tel Dor	Dor	Coastal	Iron Age II (950–539 BCE)	12
Lingrin tou Digeni	LTD	Coastal	Archaic–Classical Period (700–332 BCE)	20

Table 1. Site names, codes, dates, and sample sizes.

The sample comprises Iron Age 2 Abel Beth Maacah (ABM, N=74); Iron Age 2 Tel Dor (Dor, N=12); pooled Iron Age 2 and Persian Keisan (Keisan, N=14), and Archaic-Classical Lingrin tou Digeni (N=20). Although every effort was made to achieve a spatiotemporally balanced dataset for this analysis, the diverse zooarchaeological assemblages included in this study are not homogenous with respect to the sample size from each site and time period. In the case of Dor and Keisan, we analyzed a sample of N<15. Smaller sample sizes have been shown to be less statistically powerful in previous analyses and the results produced here should be interpreted with caution (Cardini et al., 2015; Pöllath et al., 2019). It is also worth noting that the astragali from ABM were recovered from a jar that held more than 400 astragali of diverse artiodactyls (Susnow et al., 2021), while the specimens from other sites were derived from refuse layers in a settlement context or, in the case of LTD, from a cultic context. These points will be discussed following the presentation of the results below.

Digitization. Digital photographs of the anterior surface of each astragalus were taken in ambient lighting with a Nikon D7500 using an AF-S Nikkor 40mm lens by lab technician Roee Shafir. The camera was stabilized on the photography table using a 90° stable arm. For each photo, the astragalus was placed in a sand-filled box and a bubble level was used to ensure that the surface was horizontal. A 1 cm scale was placed at the level of the photographed surface. The dataset of digital photos was imported into tpsUtil (v.147) (J. Rohlf, 2015). Digitization of landmarks was conducted by laboratory assistant Daria Loshkin Gorzilov, under the direct supervision of S. Harding, using tpsDig232 (v.231) (J. F. Rohlf, 2017). We preferred left-side elements; images of right-side elements were flipped in tpsDig 232. The landmark configuration followed the protocol outlined in Pöllath et al. (2019): 11 fixed landmarks (LM) and 14 semi-sliding

landmarks (SSLM) were placed around the outline of the dorsal view (Figure 2). A scale was set for each photo within tpsDig.

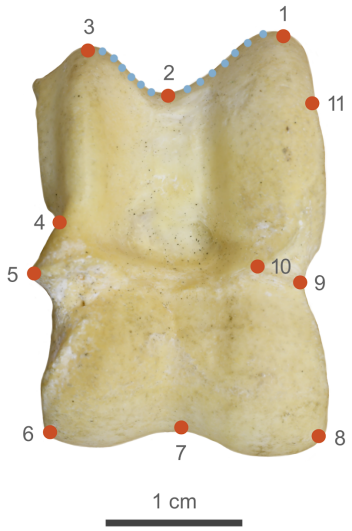

Figure 2. Landmark (red) and sliding semi-landmark (blue) placement, after Pöllath et al. (2019).

Digitization error. Digitization errors were checked before statistical analysis by using tpsSmall64 (v.1.0) and tpsrelw32 (v.1.53) (Rohlf, 2015) according to the protocol described by Adriaens (2007). A subset (N=28) of specimens from the dataset were digitized three unique times in order to test for digitization error; these were randomly selected but as evenly distributed between the study sites as possible.

Generalized Procrustes analysis. A Generalized Procrustes Analysis (GPA) was performed using the gpagen() function in 'geomorph' (Adams et al., 2022; Adams & Otárola-Castillo, 2013) on the landmark coordinates obtained in tpsDig which produced Procrustes shape variables (Bookstein, 1991). Semi-sliding landmarks were allowed to slide relative to each other during the GPA in order to minimize the sum Procrustes distances between each specimen and the mean shape (Bookstein, 1996). Centroid sizes of the specimens were also produced by the same function.

Ordination and disparity analyses. We used principal component analysis (PCA, implemented using 'geomorph::gm.prcmp') to reduce the dimensionality of the Procrustes transformed landmarks, while retaining most of the variability present among the Procrustes shapes. The first

ten principle components were used in a canonical variates analysis (‘Morpho::CVA’) to visualize group structure and measure inter-group Mahalanobis distances in the resulting ordination space. We also conducted a Procrustes disparity analysis (Zelditch et al., 2014) on the Procrustes transformed coordinates using geomorph::morphol.disparity.

R libraries. GMM analysis and visualization were conducted in R (v.4.1.0) (R Core Team, 2022) using the following packages: ‘geomorph’ (Adams et al., 2022; Adams & Otárola-Castillo, 2013), ‘Morpho’ (Schlager, 2017), ‘tidyverse’ (Wickham et al., 2019), and ‘ggsci’ (Xiao, 2018).

Results

Digitization error. Landmark digitization error was quantified by calculating the ratio of the mean Procrustes distance of the digitization error subset (mean=0.034) and the whole dataset (mean= 0.118); the percent of digitization error was 29.37%. This percentage represents the variation in the sample due to imprecision of landmark placement, which does not have a fixed value (Yezerinac et al., 1992, p. 471). This percent of digitization error is within the range expected for highly morphologically conserved skeletal elements based on other geometric morphometric studies (Hulme-Beaman, 2014, pp. 164–167).

Centroid size. Median centroid sizes are plotted in Figure 3A, and are significantly different ($P<0.001$; see ANOVA table in Supplement 1a) between sites. They suggest that slightly larger sheep were present in Tell Keisan, which is a similar result to that obtained by a biometric study of the sheep remains from the site (Harding et al., 2023). The smaller size of the Dor specimens also resonates well with the results from other Levantine coastal sites in the Iron Age (Chahoud et al., 2023). The specimens from Cyprus are especially small. We do not know how universal this pattern may be on the island during the Iron Age, and this observation requires further investigation. The effect of size on shape data is statistically significant ($P = 0.009$), but has a negligible effect ($R^2 = 0.01$) in comparison to that of group ($P = 0.001$, $R^2 = 0.11$). The effect of the interaction between group and size on shape is not significant. The full model output appears in Supplement 1.

Ordination. The group-based CVA ordination of the first ten principle components explains almost all the variability in that dataset (~98%)(Figure 3B). The ABM and Keisan specimens cluster together near the origin, with the Dor and LTD data occupying higher and lower regions

along CV1, respectively, and a higher position on CV2. The Mahalanobis distance between the groups, when presented in a dendrogram (Figure 3C), reveals a geographic structure similar to the astragular shape data. The classification output of the CVA analysis is in Supplement 1.

Disparity. The Procrustes distances between groups is presented in Table 2, and as an unrooted neighbor-joining tree in Figure 4A. The tree suggests a similar geographic structure to that obtained by the ordinated CVA results. The similarity between the results of two different analyses—direct measurements of disparity on landmark data and on eigen-ordinated coordinates—support the statistical results. A random permutation procedure produced statistically significant differences among the Procrustes distances calculated between the easternmost inland site, ABM, and the coastal samples. Finally, Figure 4C presents the intra-group variance in the Procrustes transformed landmark data in each group in relation to its sample size. Notably, the coastal assemblages have a much higher intra-sample variance than inland ABM; after normalization, the amount of variance per site can be observed to be independent of sample size.

	ABM	Keisan	Dor	LTD
ABM		0.96	*0.04*	*0.001*
Keisan	0.0000507		0.08	*0.003*
Dor	0.0020000	0.0020517		0.148
LTD	0.0037418	0.0037926	0.0017409	

Table 2. Pairwise absolute differences between sample variances (lower diagonal) and p-values (upper diagonal) obtained from a randomized residual permutation procedure ($N_{permutations}$ = 1000).

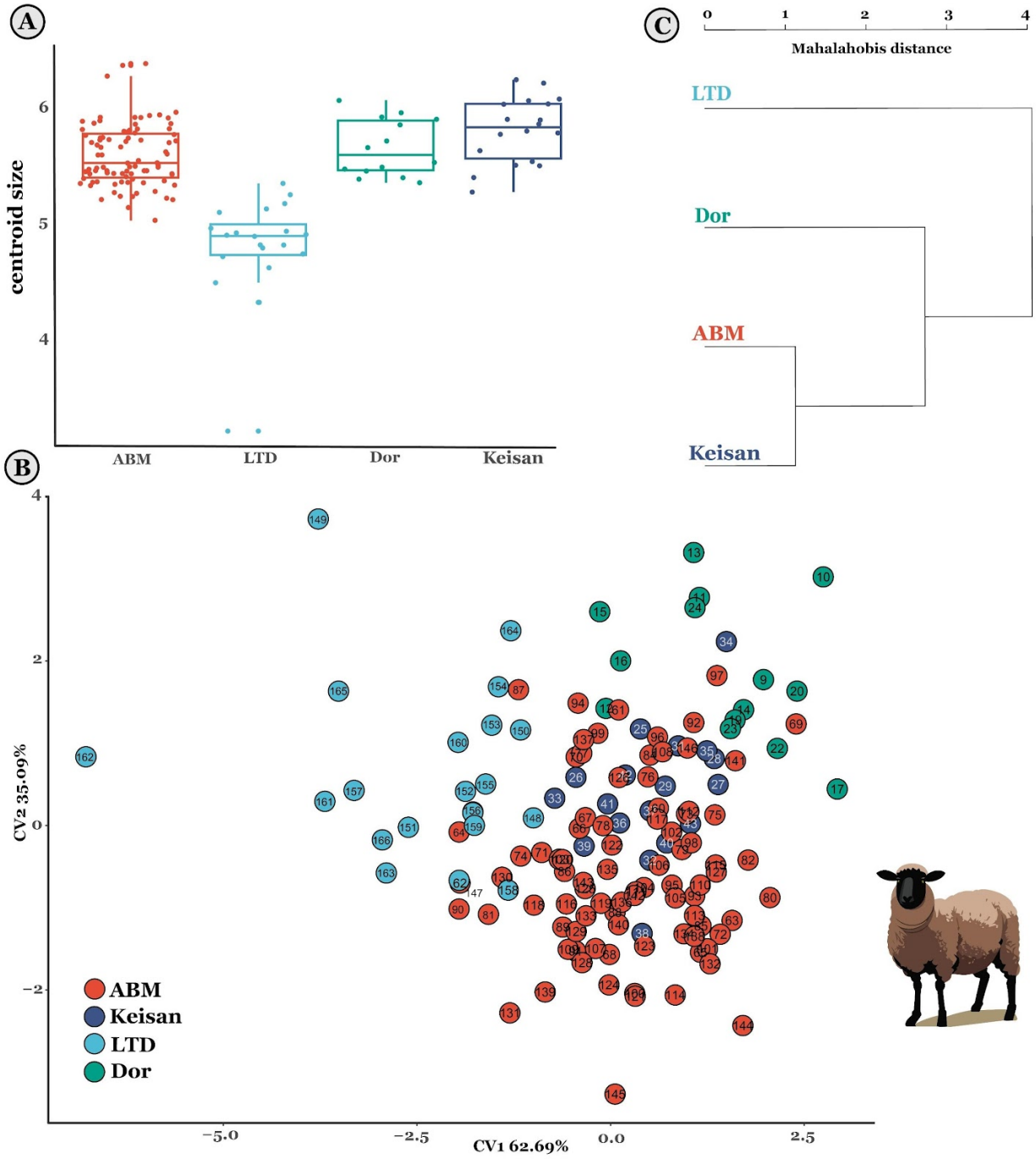

Figure 3. Boxplots present specimen centroid sizes (A) of astragali from Iron Age 2 Tel Abel Beth Maacha (ABM; n=87), Iron Age 2 Tel Dor (n=14), and the combined Iron Age 2 and Persian period samples from Tel Keisan (n=19). (B) Canonical variates ordination of the first ten principle components obtained from a shape PCA of the Procrustes transformed landmark data. (C) Dendrogram of the Mahalanobis distance between groups, calculated from the CVA ordination data. Specimen numbers refer to the specimen info file at https://zenodo.org/doi/10.5281/zenodo.10276146

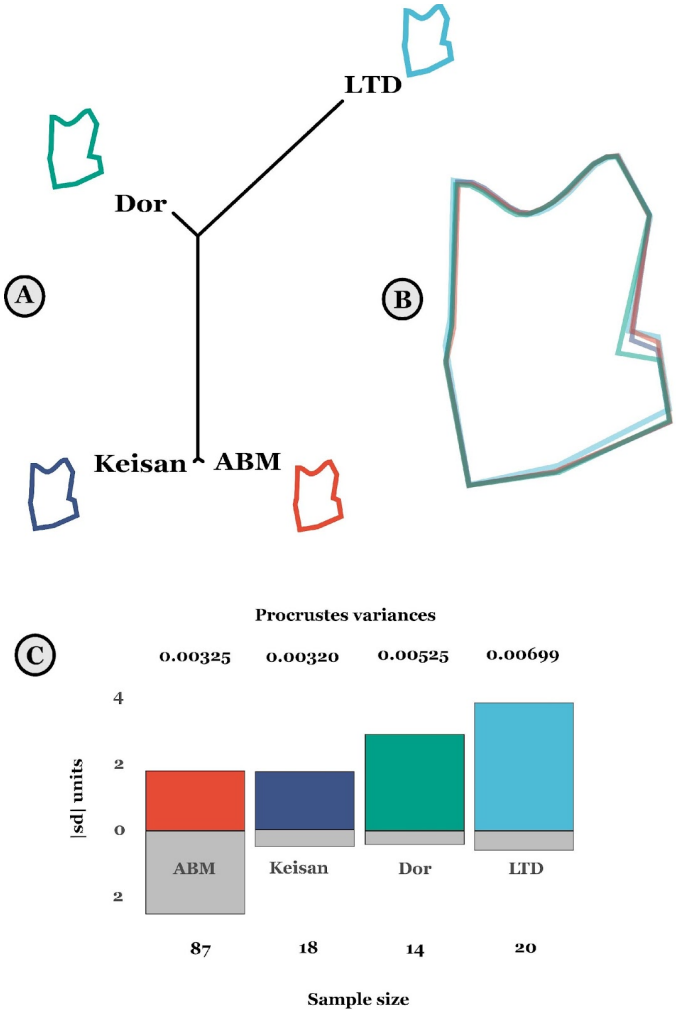

Figure 4: (A) Procrustes distances between groups presented as a neighbor-joining tree; mean shape for each group plotted separately at each tip. (B) Superimposition of the mean shapes for each group. (C) Standardized absolute Procrustes variances within each site in relation to sample size. Absolute values of the standardized columns appear above (distances) and below (sample size) their respective columns.

Discussion

Our analysis returned results related to size and shape variability within and between sites. First, with respect to size, we observe a significant difference between sites, with the Cypriot LTD showing notably smaller size than the other, southern Levantine sites. Within the other sites, our results do not contradict previous findings related to body size based on traditional biometric analyses (Chahoud et al., 2023; Harding et al., 2023). Second, morphological variability appears to be greater in coastal sites compared to inland sites. This observation does not appear to be related to sample size, as the site with the largest

sample size, ABM (N=87), has approximately half the morphological variance of LTD (N=20). Third, a clear east-west morphocline emerges: morphological similarity between sites maintains the rank order of the geographical distance between them. Significance values mark a clear similarity between Dor/LTD, the coastal sites, and ABM, the easternmost site.

The interpretation of the data could be straightforward: Samples from coastal sites reflect a broad and morphologically variable population of sheep in the Iron Age. The importance of the sea as a connective medium is apparent in that the sheep from Dor are morphologically closer to the sample from Cyprus than to inland sheep from the nearby Galilee at Tell Keisan. Higher shape diversity in the coastal, Mediterranean sites confirms the greater exposure of the sheep sampled from them to non-local animals, hence supporting our hypothesis.

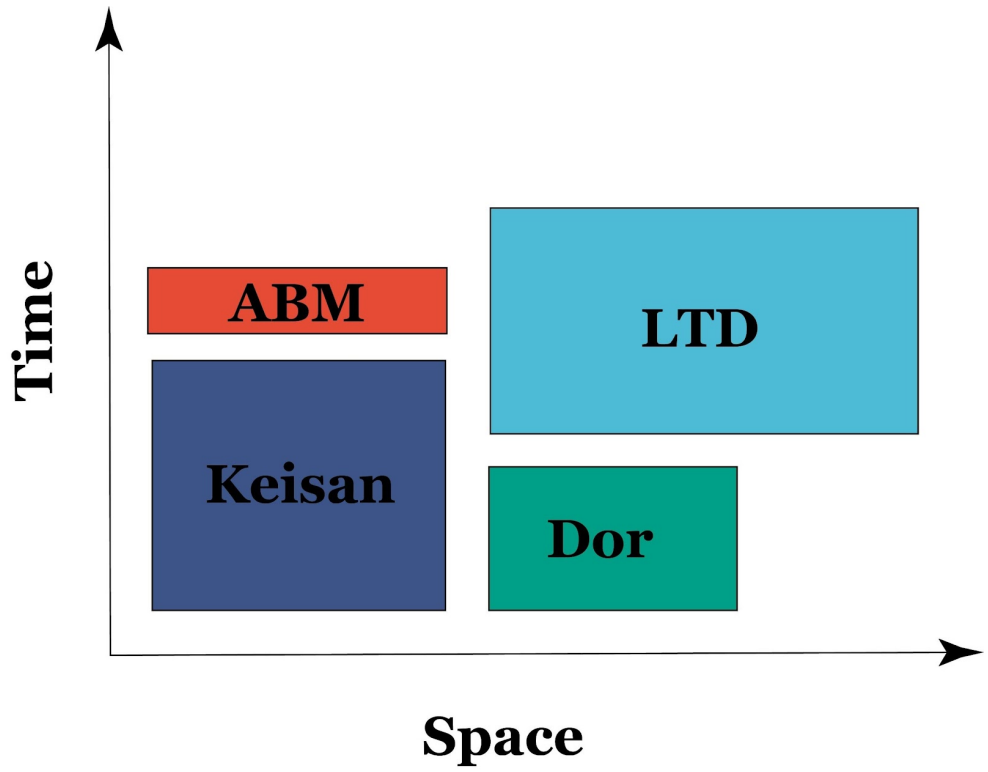

Figure 5. The effect of zooarchaeological context on intra-site shape variability when the sample sizes are similar. Rectangle area represents intra-site morphological variability, and is a function of the spatial variability (~space) of the region from which the animals were obtained (large for the ritual site of LTD) and the time period over which they accumulated (very short in ABM). We cannot at this point estimate the contribution of zooarchaeological context to the differences in the variability we analyzed in this study.

Our confidence in these conclusions is compromised by issues of zooarchaeological context (Figure 5): we are not sure that the different samples we obtained represent the variability in the geographical region

from which they derive in the same way. The large sample from ABM was obtained from a single jar, used as a ‘favissa’ to astragali of different taxa. Even if we accept that the astragali represent random mortality from herds living in the agricultural hinterland of the site, the sample is extremely confined in the temporal sense, because it represents the total collection time of a complete jar, which we estimate in years. This stands in contrast with the longer, decadal or centennial scale accumulations of refuse buried in Keisan and Dor which sample a larger span of time. Regarding spatial variability, in LTD, the high intra-assemblage variation may be due to the ritual activities. These work as a sink for livestock variability, as people came from variable distances to make offerings. Such considerations complicate interpretation, especially on the intra-site variance comparisons. We tend to think that inter-site patterns of variation, especially the inland versus coastal morphotypes, should be more robust.

At this point, therefore, our results support the idea that maritime connectivity is related to morphological variability in Iron Age livestock, but with the important caveats mentioned above. The way forward would be to enlarge the number of sampled sites focusing on material recovered from accumulated deposits, thereby eliminating, or much reducing, idiosyncrasies related to zooarchaeological context.

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Conflict of interests disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Data availability

R codes, TPS files and a specimen catalogue are available at

https://zenodo.org/doi/10.5281/zenodo.10276146

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